

# Pyropeltidae, a New Family of Cocculiniform Limpets from Hydrothermal Vents

by

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**Abstract.** A new genus, *Pyropelta*, is proposed for two new species from hydrothermal vents: the types species, *P. musaica*, from the Juan de Fuca Ridge off Washington, and *P. corymba*, from the Guaymas Basin in the Gulf of California. Shells resemble some genera of Pseudococculinidae in having a similar pattern of erosion. Absence of cephalic lappets, differences in the excretory system, presence of an osphradium, and major differences in the radula warrant recognition of the new family Pyropeltidae for the genus. Relationships of the Pyropeltidae among the Lepetellacea are discussed, with comparisons to those families with a similar radula (Pseudococculinidae, Osteopeltidae). The two species live directly on sulfide crust, unlike all other Lepetellacea, which are usually associated with biogenic substrata.

## INTRODUCTION

The hydrothermal-vent environment has yielded a number of remarkable discoveries among mollusks. Although limpets of a number of families are well represented (McLEAN, 1985b), the presence of cocculiniform limpets in the hydrothermal-vent habitat had not been recognized until now. In a preliminary report on limpets of the hydrothermal vents, McLEAN (1985b) noted the absence of members of this group, a generalization that is here emended. Large numbers of one new species described here were first collected at the Juan de Fuca Ridge by the submersible *Pisces IV* in July 1986. A single specimen of a species from the Guaymas Basin had been collected in January 1982, but its radula was not examined and its affinity not ascertained until now.

The cocculiniform limpets include the families Cocculinidae Dall, 1881; Lepetellidae Dall, 1882; Addisoniidae Dall, 1882; Bathysciadiidae Dautzenberg & Fischer, 1900; Cocculinellidae Moskalév, 1971; Bethyphytophilidae Moskalév, 1978; Pseudococculinidae Hickman, 1983; and Osteopeltidae Marshall, in press. One family with coiled

shells has been recognized, the Choristellidae Bouchet & Warén, 1979. These families have recently received new attention, starting with papers by MOSKALEV (1971, 1973, 1976, 1978) and followed by HICKMAN (1983) who gave the first SEM illustrations of radulae, and papers by MARSHALL (1983, 1986) and McLEAN (1985a). HASZPRUNAR (1987, in press a, b, c, d) has anatomical studies underway relating to these families.

In this paper another cocculiniform family is described. It has a distinctive radular plan and unique combinations of anatomical characters, and it does not require a substrate of biological origin. Other families of cocculiniform limpets occur and feed upon a variety of substrates including wood or other plant material, polychaete tubes, bone, cephalopod beaks, crab exoskeletons, and elasmobranch egg cases.

Type material is placed in the Los Angeles County Museum of Natural History (LACM), the Museum National d'Histoire Naturelle, Paris (NMNH), the National Museum of Natural History, Washington, D.C. (USNM), and the National Museum of New Zealand, Wellington (NMNZ).

## TAXONOMY

## Superfamily LEPETELLACEA

Limpets with horseshoe-shaped muscle, lacking juvenile coiling, or coiled with a single (left) shell muscle (Choristellidae only). With or without oral lappets and epipodial tentacles. Several secondary gill-leaflets (pallial and/or subpallial). Heart monotocardian. Two kidneys, the left one small or vestigial and usually connected with the pericardium, the right one larger and isolated. Limpet families hermaphroditic with separated, ventral testis, and dorsal ovary; right cephalic tentacle often serving as copulatory organ, never with copulatory verge proper; open or closed seminal groove at right neck; gonoduct(s) without glands. Statocysts with several or many cones. Rachidian tooth of radula well developed.

**PYROPELTIDAE** McLean & Haszprunar, fam. nov.

Because a single genus in this new family is presently known, the generic description and discussion serve for that of the family.

***Pyropelta*** McLean & Haszprunar, gen. nov.

Type species: *Pyropelta musaica* sp. nov.

**Diagnosis:** Shell small for superfamily (maximum length 4.6 mm), white, periostracum unknown (probably worn off). Apex central, at highest elevation of shell. Protoconch and exterior sculpture eroded. Exterior surface of shell etched with irregular concentric lines reflecting uneven erosional pattern. Shell margin thin, fragile. Shell interior with pattern of concentric, wavy, alternating light and dark reflective areas, a pattern not corresponding to the exterior pattern of irregular concentric lines. Muscle scar closer to mid-point of shell than to margin; anterior tips of scar broadly inflated, tips projecting inward. Muscle scar continuous anteriorly with pallial attachment scar, which together with muscle scar makes a continuous oval scar. Surface central to scar areas thickened, opaque white. Interior muscle scar pattern visible externally through translucent shell.

**Radula.** Rachidian tooth broad, with rounded lateral extremities, tapered base, and long, tapered neck, with small overhanging tip. Shaft and base of first lateral broad, inner edge excavated to accommodate base of rachidian, upper portion of shaft tapering to long overhanging cutting area. Second and third laterals largest, similar, each with pronounced elbow on outer side and deeply grooved upper arm of shaft for accommodation of adjacent teeth; cutting area long, serrated, tip rounded. Fourth lateral unlike first three, shaft broad, lacking elbow, its cutting area concavely arched and serrate on inner side. Fifth lateral similar to fourth in having broad shaft and undulating cutting edge, its tip with projecting cusps. Lateromarginal plate elongate (visible from basal side of ribbon), positioned between tooth rows. Marginal basal plate present; marginals numerous,

not separated at base, first and second marginal not enlarged.

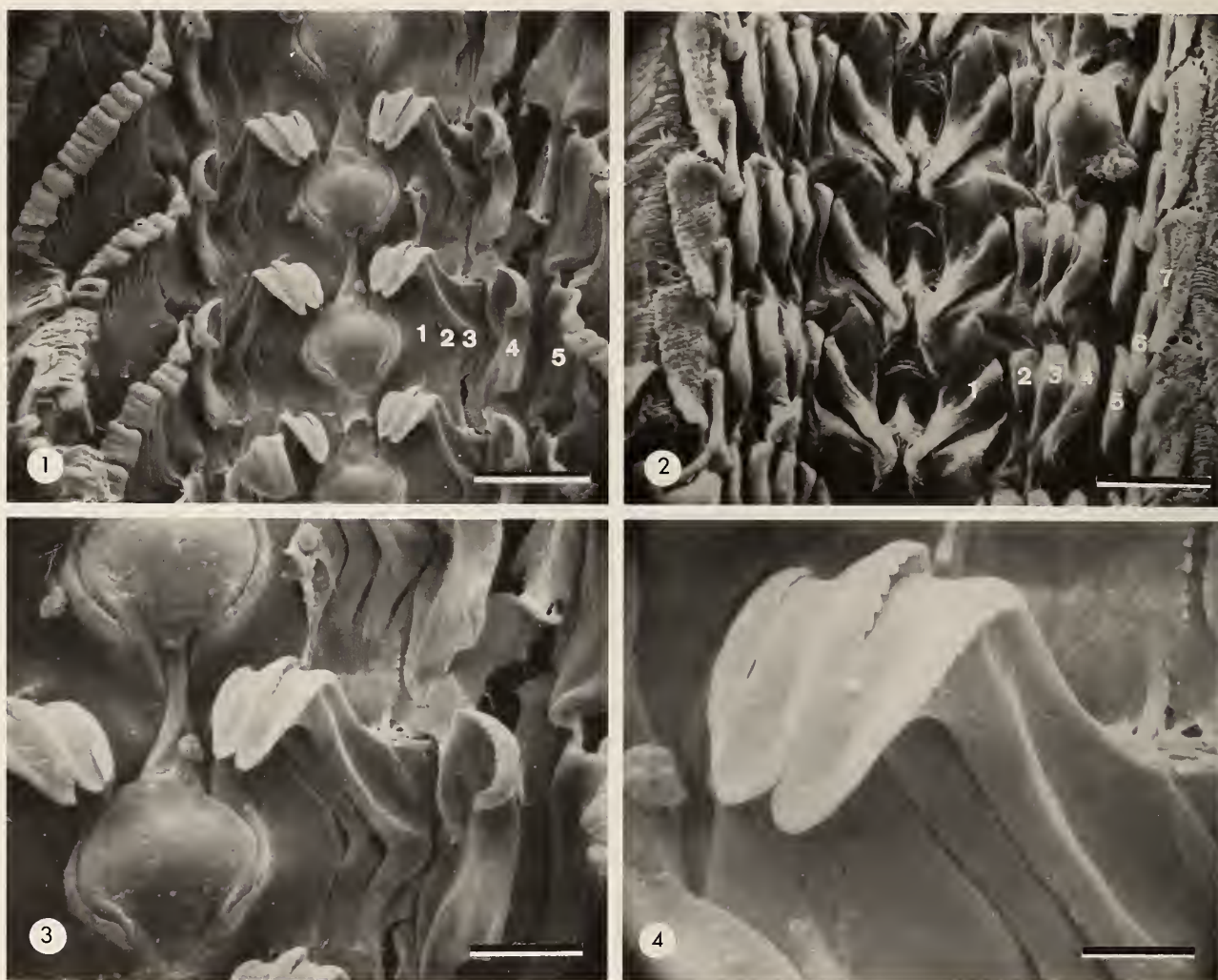
**External anatomy.** Oral disc broad, circular, lappets lacking; cephalic tentacles equal, like the mantle devoid of papillae. No subpallial glands. Foot with deeply contracted central area. Posterior pair of epipodial tentacles present. Gill tips especially prominent on right side; mantle skirt above neck thin. Right cephalic tentacle (copulatory organ) simple and solid; from its base an open seminal groove leads to the genital opening along right neck.

**Internal anatomy.** Two uninterrupted shell muscles forming a horseshoe-shaped organ, the left muscle slightly larger than right. Pedal gland small but distinct. Mantle cavity shallow, from left (in dorsal view) a distinct osphradium, pericardium, left kidney, anus, right excretory/genital opening, and genital gland. No hypobranchial gland. Secondary gill leaflets up to 18, at central and/or right pallial roof, continuing into right subpallial cavity. Gill leaflets respiratory and provided with sensory pockets. Heart monotocardian, pericardium large, ventricle posterior to auricle. Left kidney extremely small and vestigial (max. dimension  $100 \times 60 \times 30 \mu\text{m}$ ), isolated. Right kidney forms large coelomic system; fused with single and simply ciliated gonoduct immediately at common opening. Testis ventral, ovary dorsal, more posterior, separated, no accessory glands or vesicles along common gonoduct. Eggs large and yolk-rich, no allosperm observed. From excretory/genital opening a glandular open duct runs forwards to anterior end of right shell muscle, further continued by seminal groove. Jaws paired, consisting of toothlike elements. Sublingual cavity shallow, no subradular organ. Two pairs of cartilages, posterior pair smaller, radular diverticulum present. Salivary glands paired, pouchlike. Anterior oesophagus broad, with dorsal food channel and pouches. Folds of channel posteriorly fused during oesophageal torsion. Stomach with gastric shield and tooth, lacking protostyle, with paired mid-gut glands, the right enlarged anteriorly. Several intestinal loops, rectum penetrating ventricle. Nervous system streptoneurous, hypopharyngeal, with pedal ganglia (two commissures), visceral ganglia indistinct; a single (left) osphradial ganglion. No eyes or optic nerve; osphradial epithelium well developed; statocysts with several statocones.

**Remarks:** Two species are known, the type species from hydrothermal vents on the Juan de Fuca Ridge off Washington, and *Pyropelta corymba* from hydrothermal vents in the Guaymas Basin, Gulf of California. *Pyropelta* is the only hydrothermal vent limpet not known from either of the two sites on the East Pacific Rise (near 21°N and 13°N), where 14 limpet species are known from each site (McLean, 1985b).

Exterior surfaces of both species are eroded, but this is probably normal for the genus. It is compensated by thickening of the shell from within. Such erosion also takes place in other deep-sea habitats and is usual in many pseudococculinid species.





Explanation of Figures 1 to 4

Figures 1 to 4. SEM views of radula of *Pyropelta musaica* sp. nov. Lateral teeth numbered 1 through 5; 6 = lateromarginal plate; 7 = marginal basal plate.

Figure 1. Rachidian, laterals, and marginals. Bar = 20  $\mu$ m.

Figure 2. Basal view, showing rachidian, laterals, lateromarginal plate, and marginal basal plate. Bar = 20  $\mu$ m.

Figure 3. Rachidian and laterals. Bar = 10  $\mu$ m.

Figure 4. Laterals 1, 2, and 3. Bar = 4  $\mu$ m.

*Pyropelta musaica* McLean & Haszprunar, sp. nov.

(Figures 1–8, 9A)

**Description:** Shell (Figures 5, 7, 8) small (maximum length 4.6 mm), white, periostracum unknown (probably eroded). Height low to moderate, that of holotype 0.26 times length. Apex central, at highest elevation of shell. Protoconch and exterior sculpture entirely eroded. Exterior surface of shell etched with irregular concentric lines reflecting uneven erosional pattern. Shell margin thin, fragile; plane of aperture nearly flat in shells of oval outline; laterally compressed forms have ends raised relative to sides. Muscle scar pattern visible from exterior through translucent shell;

muscle closer to mid-point of shell than to margin; anterior tips of scar broadly inflated, tips projecting inward. Shell interior with pattern of concentric, wavy, light and dark reflective areas, not corresponding to exterior pattern of irregular concentric lines. Shell thin and transparent enough to reveal the exterior pattern from inner side. Muscle scar of interior as described above, continuous anteriorly with pallial attachment scar, which together with muscle scar makes a continuous oval scar. Surface central to scar areas thickened, opaque white.

**Dimensions.** Length 3.0, width 2.7, height 1.0 mm (holotype).

**Radula** (Figures 1–4) described above under generic heading.



Explanation of Figures 5 to 8

Figures 5 to 8. *Pyropelta musaica*.

Figure 5. Holotype. Exterior, interior (anterior at top), and lateral (left side) views of shell. Length 3.0 mm.

Figure 6. Holotype body out of shell, dorsal and lateral (right side) views, showing gill lamellae projecting on right. For orientation see Figure 9A. Length 1.9 mm.

Figure 7. Ventral view of paratype showing light and dark reflective areas of shell interior. Length 3.2 mm.

Figure 8. Ventral and dorsal views of paratype (laterally compressed form). Length 3.1 mm.



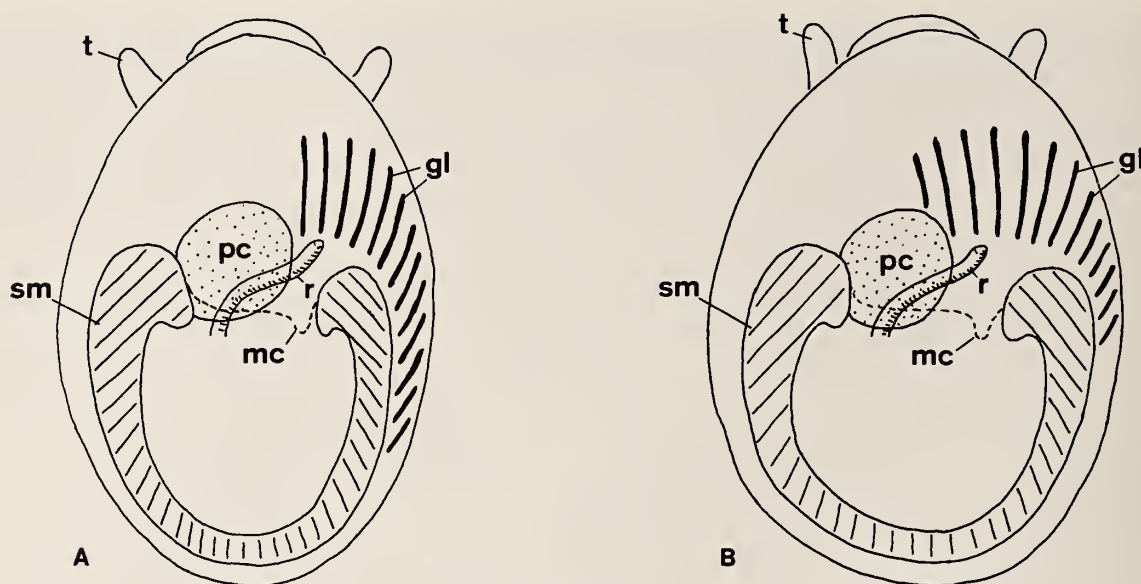


Figure 9

Comparison of arrangement of gill-leafflets in *Pyropelta* species. Dorsal view, schematic. A. *P. musaica*. B. *P. corymba*. Abbreviations: gl, gill leafflets; mc, posterior end of mantle cavity; pc, pericardium; r, rectum; sm, shell muscle.

**External anatomy** (Figures 6–8, 9A) described under generic heading.

**Internal anatomy** described under generic heading. For purposes of comparison with *Pyropelta corymba*, the left kidney of *P. musaica* is extremely small ( $30 \times 50 \times 30 \mu\text{m}$ ). Gill leafflets up to  $25 \mu\text{m}$  long at right pallial roof, reaching posteriorly in right subpallial cavity up to two-thirds of body length (Figure 9A). Anterior edge of shell muscles not specialized.

**Type locality:** Axial Seamount, Juan de Fuca Ridge, off Washington ( $45^{\circ}59.5'N$ ,  $130^{\circ}03.5'W$ ), 1575 m.

**Type material:** Holotype and paratypes from 6 *Pisces IV* dives, July–August 1986, depth and coordinates as above. Holotype from dive 1733, paratypes from following dives: 6 specimens, dive 1723, Hammond's Hell Vent, 19 July; 10 specimens, dive 1728, Southern Axial Vent, 29 July; 16 specimens, dive 1729, Anemone Ridge, 30 July; 8 specimens, dive 1730, Eastern Axial, 31 July; 1 specimen, dive 1731, Post Taylor's Vent, 1 August; 50 specimens, dive 1733, Not-so-miserable Vent, 3 August. Holotype, LACM 2275 (dive 1733); 65 paratypes LACM 2276; 10 paratypes USNM 784760, 10 paratypes MNHN; 5 paratypes NMNZ. Specimens from dive 1733 were sectioned.

**Etymology:** The name is Latin for *mosaic*, with reference to both the exterior erosional pattern and the interior banding pattern.

**Remarks:** In addition to radular differences, *Pyropelta musaica* may be distinguished from pseudococculinid species on its generic characters—the pattern of light and

dark banding on the shell interior, and the lack of oral lappets. Although the shell is variable in height, the most elevated specimens are not as high as the single specimen of *P. corymba* sp. nov.

There is a considerable range of expression in apertural shape, ranging from broadly oval (Figure 5) to laterally compressed, with more elevated ends (Figure 8). Some shells, as for example the holotype (Figure 5), change during growth from somewhat compressed to lower and more oval. This range of variation in apertural shape suggests that individuals are adapted to a habitual site of attachment, which they may leave in foraging for food.

General descriptions of the biota at Axial Seamount (the type locality) are given by CHASE *et al.* (1985) and TUNNICLIFFE *et al.* (1985), although the existence of *Pyropelta musaica* is not mentioned, as it had not been collected prior to 1986. According to V. Tunnicliffe (personal communication), these limpets live “in the warm water vents and on surrounding rocks.” They were apparently not collected directly from washings of the vestimentiferan tubes. The species has not been found at the Explorer Ridge farther to the north. One other much larger limpet (description by McLEAN, in press) is common at all sites on the Juan de Fuca and Explorer ridges.

*Pyropelta corymba* McLean & Haszprunar, sp. nov.

(Figures 9B, 10, 11)

**Description:** Shell (Figure 10) small (maximum length 3.0 mm), white, periostracum lacking. Elevation extremely high, that of holotype 0.83 times length. Apex posterior,



Explanation of Figures 10 and 11

Figures 10 and 11. *Pyropelta corymba* sp. nov. Holotype.

Figure 10. Exterior, interior (anterior at top), and lateral (left side) views of shell. Length 3.0 mm.

Figure 11. Ventral (in shell) and lateral views of body (left side) prior to sectioning. For orientation see Figure 9B.

at highest point of shell, two-thirds shell length from anterior margin. Protoconch and exterior sculpture eroded, no evidence of sculpture on exterior surface. Exterior surface of shell etched with irregular concentric lines reflecting uneven erosional pattern. Shell margin thin, easily broken; plane of aperture with ends raised relative to sides. Shell interior with pattern of concentric, wavy alternating light and dark reflective areas, not corresponding to the exterior pattern of irregular concentric lines. Shell thin and transparent enough to reveal the exterior pattern from inner side. Muscle scar closer to mid-point of shell than to margin; anterior tips of scar broadly inflated, tips projecting inward, continuous anteriorly with pallial attachment scar, which together with muscle scar makes a continuous oval scar. Surface central to scar areas thickened, opaque white. Muscle scar pattern apparent on exterior of shell.

*Dimensions.* Length 3.0, width 2.5, height 2.5 mm (holotype).

*Radula* not available (specimen sectioned).

*External anatomy* (Figure 11) as described for the genus.

*Internal anatomy* as described for the genus. For comparison with *Pyropelta musaica*, the left kidney of *P. corymba* is larger ( $100 \times 60 \times 40 \mu\text{m}$ ). Gill leaflets up to  $60 \mu\text{m}$  long, extending from central pallial roof to the right, reaching posteriorly in right subpallial cavity up to one-half body length (Figure 9B). Anterior edge of shell muscles bordered by a strongly ciliated epithelial ridge.

**Type locality:** Southern trough of Guaymas Basin, Gulf of California, off Guaymas, Sonora, Mexico ( $27^{\circ}01.0'N$ ,  $111^{\circ}25.0'W$ ), 2022 m.

**Type material:** 1 specimen from type locality, *Alvin* dive



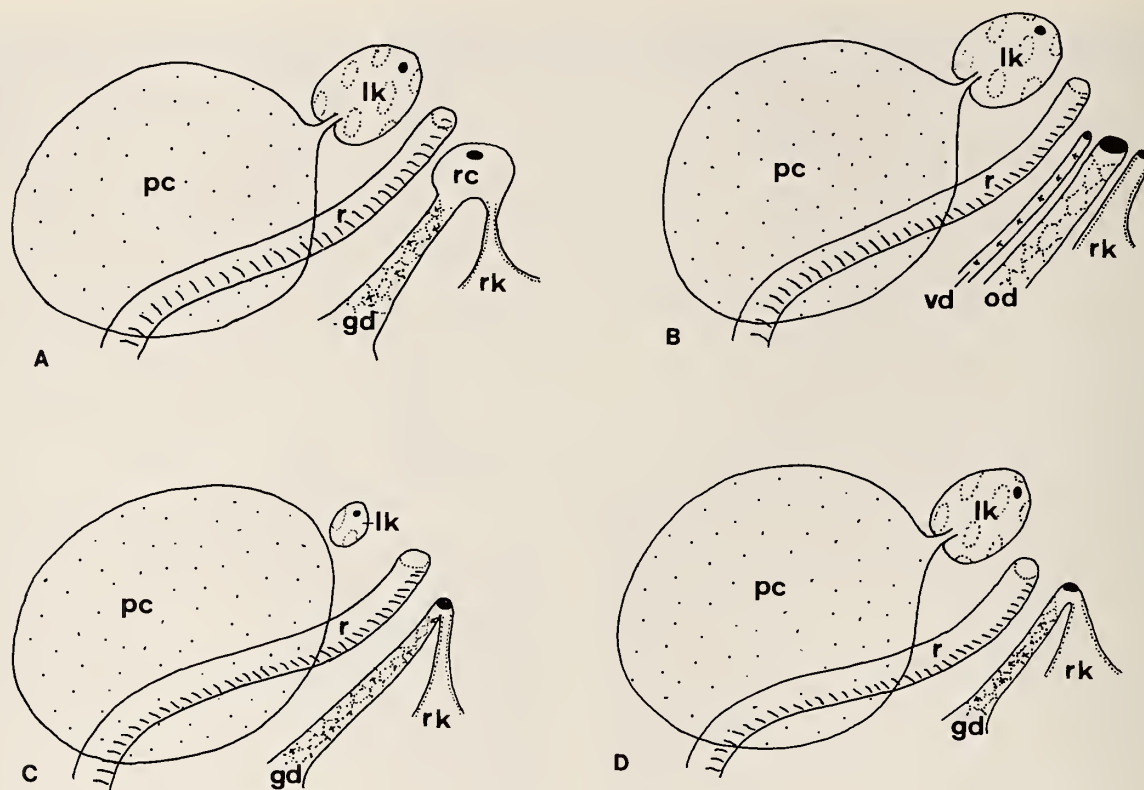


Figure 12

Comparison of coelomic systems of lepetellacean families. A. Lepetellidae. B. Osteopeltidae, Cocculinellidae, and Addisoniidae. C. Pyropeltidae. D. Pseudococculinidae. Abbreviations: gd, gonoduct; lk, left kidney; od, oviduct; pc, pericardium; r, rectum; rc, releasing chamber; rk, right kidney; vd, vas deferens.

1176, 19 January 1982. Holotype, LACM 2277. No other specimens are known. The body of the holotype has been sectioned.

**Etymology:** The name is derived from Greek, *corymbos*, peak, with reference to the high profile of the shell.

**Remarks:** The shell meets the generic criteria for *Pyropelta* in being relatively small, with exterior erosion as well as the interior pattern of alternating light and dark reflective areas. It differs from *P. musaica* in having a much higher profile and a more posterior apex. The left kidney is larger, the gill leaflets are longer, and the anterior edge of the shell muscle is bordered by a strongly ciliated epithelial ridge (unspecialized in *P. musaica*).

Although the height of the single specimen places it well outside the range of variation noted in *Pyropelta musaica*, it is impossible to tell in the absence of additional material whether this specimen represents the extreme or the norm.

One other limpet (described by McLEAN, in press) is known from the Guaymas Basin site. A general description of the hydrothermal site and its biota was given by LONSDALE (1984).

This species has previously been cited (McLEAN 1985b:

160, 162) under the vernacular name "Group-C, high-conical." There is no affinity to other Group-C limpets (terminology of HICKMAN, 1983) for which the descriptions are now in preparation by McLEAN, the anatomy under study by V. Fretter. The lack of cephalic lappets led to that assignment, but the radula and anatomy were not examined at that time.

## DISCUSSION

### Systematic Position

The shell and anatomy of *Pyropelta* fall well within the lepetellacean "bauplan" (see above definition of superfamily). Affinity is closest to the Pseudococculinidae and Osteopeltidae on the basis of similarities in the shell, radula, and gill leaflets. The erosional pattern of the shell and corresponding prominence of the muscle scar occurs in typical species of the Pseudococculinidae. Except for the lack of cephalic lappets and the lack of papillae on the cephalic tentacles and mantle margin (both also absent in *Osteopelta* Marshall, in press), the features of the external anatomy also agree with what is known of pseudococculinids.

The internal anatomy of *Pyropelta* also resembles that of the Pseudococculinidae. However, all characters in common are regarded as primitive (plesiomorphic) for the Lepetellacea (HASZPRUNAR, in press d), including the presence of sensory pockets at the efferent axes of the gill-leaflets (such pockets also occur in the Lepetellidae; unpublished observation of G.H. on three species in two genera).

Differences from the Pseudococculinidae are found especially in the excretory system. The Pseudococculinidae, as well as other lepetellacean families so far investigated, have a small, but distinct left kidney, which communicates with the pericardium (Figure 12D). In contrast, the left kidney of *Pyropelta* is extremely small, vestigial, and isolated (Figure 12C). This reduction resembles that of the Fissurellacea (ANDREWS, 1981, 1985). The reasons for these reductions are unknown in either family.

In contrast, the relation between the right kidney and the genital system is the same in *Pyropelta* and in the Pseudococculinidae. In both families the right kidney is fused with the genital duct immediately at the common opening (Figures 12C, D). The condition is more derived than that in the Lepetellidae, in which the distal portions of the right kidney and the distal genital duct form a releasing chamber that differs in histology from both organs (Figure 12A). The final condition among the Lepetellacea is represented by *Osteopelta* Marshall, in press, *Cocculinella* Thiele, 1909, and *Addisonia* Dall, 1882 (HASZPRUNAR, 1987, in press b, d). There the common gonoduct is separated into vas deferens and oviduct, and three independent openings exist (Figure 12B). Thus, *Pyropelta* and the Pseudococculinidae represent an intermediate state with respect to coelomic conditions. Similar trends (common distal releasing chamber or duct—common opening—separate openings, male and female ducts) also occur among the Bivalvia (MACKIE, 1984).

There are major differences between the radula of *Pyropelta* and that of pseudococculinids. *Pyropelta* agrees with the pseudococculinid plan in having a broadly inflated rachidian and the first lateral has the broad shaft and elbow characteristic of pseudococculinids. As in the Pseudococculinidae (and unlike the Cocculinidae), the lateromarginal plate and marginal basal plate are present. It differs from the general plan in having long overhanging cutting areas on the first three pairs of laterals. The fourth lateral of *Pyropelta* is an independent element that more closely resembles the fifth, outer lateral; in pseudococculinids the fourth lateral is similar to the second and third laterals and has a pronounced elbow. Marginal teeth of *Pyropelta* also differ; inner marginals, particularly the second pair, are not enlarged as in some pseudococculinids. In some pseudococculinid genera, the enlarged cusps of the second pair of marginals make them the largest and most potentially functional teeth; in *Pyropelta*, the three inner laterals are the most effective teeth in the row.

The osteopeltid radula differs from both the pseudo-

cocculinid and pyropeltid radula in lacking marginal basal plates (see MARSHALL, in press). As in the Pseudococculinidae, the osteopeltid radula has a massive fifth lateral. It is unique in having a massive first lateral.

The alimentary tract of *Pyropelta* strongly resembles that of the Pseudococculinidae, being primitive for the superfamily (HASZPRUNAR, in press c). The only difference is the presence of two mid-gut glands, whereas only one exists in the Pseudococculinidae. *Osteopelta* differs in its specialized buccal apparatus (a single pair of cartilages only) and in having distinct oesophageal glands instead of pouches.

Most features of the nervous system of *Pyropelta*, as well as the Pseudococculinidae, reflect primitive lepetellacean conditions, whereas *Osteopelta* has a concentrated cerebropedal ring (HASZPRUNAR, in press a). Like *Cocculinella* the pedal cords of *Pyropelta* are concentrated and represent true ganglia with only two commissures. As is typical for lepetellacean limpets, there is a single (left) osphradial ganglion. However, *Pyropelta* still has retained an osphradial epithelium, whereas the Pseudococculinidae generally lack it. Otherwise the sense organs (lack of eyes, a single posterior pair of epipodial tentacles, lack of subradular organ, statocysts with several statoconia) are typical for the Lepetellacea. The presence of oral lappets is regarded as primitive for cocculiniform limpets and for archaeogastropods in general (HASZPRUNAR, in press d). Among the Lepetellacea, these lappets are lost in certain Lepetellidae (MOSKALEV, 1978) and in the derived lepetellacean families Osteopeltidae, Cocculinellidae, and Addisoniidae (HASZPRUNAR, 1987, in press b, d).

Summing up, *Pyropelta* is obviously closely related to the Pseudococculinidae. However, the lack of cephalic lappets, and the absence of sensory papillae on the cephalic tentacles and mantle margin, the major differences in the radula, the vestigial left kidney, the existence of pedal ganglia, and a distinct osphradial epithelium warrant the recognition of the new family Pyropeltidae. Moreover, the condition of the right excretory/genital system places the family closest to the Pseudococculinidae (shell muscles solid, right kidney forming a large coelomic system), but at present it cannot be decided which family first split off. The Lepetellidae (still with muscle bundles, releasing chamber, small and compact right kidney) are clearly more primitive than both, whereas the remaining lepetellacean families Osteopeltidae, Cocculinellidae, Addisoniidae, and Choristellidae, with distinct oesophageal glands and completely separated gonoducts, are more highly derived than *Pyropelta* and the Pseudococculinidae (HASZPRUNAR, in press d). Thus, the sequential (*sensu* WILEY, 1981) arrangement of lepetellacean families is now as follows: Lepetellidae, Pseudococculinidae, Pyropeltidae, Osteopeltidae, Cocculinellidae, Addisoniidae, and Choristellidae; the poorly known Bathyphytophilidae may belong here. The Cocculinidae and Bathysciadiidae together comprise the Cocculinacea (HASZPRUNAR, in press a).



## Biology and Evolutionary History

*Pyropelta* appears to be unique among cocculiniform limpets in living directly on a non-biological substrate—the sulfide crust deposits of deep-sea hydrothermal vents. Other cocculiniform limpets live and feed on such substrates as wood, cephalopod beaks, whale or fish bone, and elasmobranch egg cases. The hydrothermal-vent habitat has an abundant food source in the chemoautotrophic bacteria that proliferate on surfaces exposed to vent water. This food source would not require the specialization necessary for feeding on the harder substrates utilized by other members of the suborder, although such substrates may be weakened by bacterial activity.

It could be argued that the unspecialized feeding of *Pyropelta* reflects the basal biology of the Lepetellacea and Cocculinacea. This view is supported by the pyropeltid radula, which seems more primitive than that of the pseudococculinids in having functional lateral teeth (the long overhanging cutting edges, contrasting with the small, hook-shaped cutting edges of pseudococculinids) and unspecialized marginal teeth. Also, the remaining alimentary tract of *Pyropelta* is primitive for lepetellaceans, but this is less significant, considering that certain pseudococculinids with specialized feeding (e.g., *Tentaoculus neolithodica* on carapaces of deep-sea stone crabs, MARSHALL, 1986) also have a primitive alimentary tract (HASZPRUNAR, in press c).

However, considering that Pseudococculinidae, the most primitive family of Lepetellacea, and Cocculinidae, the most primitive family of Cocculinacea, feed predominantly on wood, wood-feeding was probably basic to cocculiniform evolution (HASZPRUNAR, in press d). Moreover, the lack of oral lappets, a derived condition, favors the secondary nature of the feeding biology of *Pyropelta*. Thus, it seems more likely that the hydrothermal-vent habitat and nourishment of *Pyropelta* are secondary for the Lepetellacea.

Although most other hydrothermal-vent limpets are probably descendents of shallow-water ancestors (MCLEAN, 1981, 1985b, in press), *Pyropelta* has its closest relatives, the Pseudococculinidae, among typically deep-water to abyssal forms. Of the other mollusks in this habitat, the turrid gastropods and most of the bivalves also are related to deep-water genera (TURNER *et al.*, 1985). The hydrothermal-vent habitat has evidently been invaded by different groups from different habitats at different times.

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